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STUDIES ON MARINE BRYOZOA. IX. *PHYLACTELLIPORA*

MARY D. ROGICK

Department of Biology, College of New Rochelle, New Rochelle, New York

The purpose of this paper is to: 1. report the occurrence of *Phylactellipora lyrulata* (Calvet) 1909 from new Antarctic localities; 2. fill in several gaps in the morphology of this species, particularly as regards orifice structures, operculum, digestive tract anatomy and skeletal wall; 3. modify the observations of Livingstone on the soft parts, observations which must have been made on polypides that were either dried up or in poor condition; 4. draw attention to the range of variation of structures; 5. bring the synonymy up to date; and 6. add to the ecology of the species.

SYSTEMATICS

Because of the recent erection of a new family Phylactelliporidae and a new genus by Dr. Bassler (1953, p. G217) the present species, heretofore known as *Phylactella lyrulata* Calvet 1909 should be assigned to Bassler's new genus *Phylactellipora*. Its classification therefore is: *Phylactellipora lyrulata* (Calvet) 1909, Family Phylactelliporidae Bassler 1953, Suborder Ascophora Levinsen 1909, Order Cheilostomata Busk 1852.

Family **Phylactelliporidae** Bassler 1953

Family Phylactelliporidae was established by Dr. Bassler (1953, p. G217) for seven genera which have a "well-developed peristomie bearing a protective organ (lyrula, mucron) for the compensatrix." The chief difference between the Phylactelliporidae and the older family Phylactellidae from which it was split off appears to be the presence of the "protective organ (lyrula, mucron)" in the new family and its absence in the now restricted family Phylactellidae. The status and comprehensiveness of the two families will undoubtedly be changed when some of the genera, particularly *Perigastrella*, and species in the family Phylactellidae Canu and Bassler 1917 are more critically studied by other workers. Time does not permit such digression so it was thought best to put the present species *P. lyrulata* into the new genus and new family and leave the more critical study of family status to subsequent workers.

Genus *Phylactellipora* Bassler 1953

Dr. Bassler (1953, p. G217) defines the genus *Phylactellipora* thus: "Zooecia with circular aperture, bearing cardelles and a lyrula. Peristome funnel-shaped, ovicell salient, globular." The type species is given as *Lepralia collaris* Norman 1867 but *Lepralia eximia* Hincks 1860 would have made a more suitable genus than the *L. collaris* because *L. eximia* has a clearly visible lyrula (see figures of both species in Hincks, 1880, pp. 358, 359 and Plate 43, fig. 3; Plate 49, fig. 9). The *P. lyrulata* is closely allied to the *L. eximia* which Hincks moved to *Phylactella* (1879, p. 161) and which Canu and Lecointre (1930, p. 108) shifted to *Perigastrella*. *Lepralia eximia* Hincks 1860 seems to belong in *Phylactellipora*.

Phylactellipora lyrulata (Calvet) 1909
(Figures 1–21)

Synonymy and previous records:

1909. ? *Phylactella lyrulata.* Calvet, p. 32; Pl. III, Fig. 7. Calvet pictured seven non-ovicelled zooecia from frontal aspect. Did not see ovicells. Mentioned lyrula but did not picture it. Had only one small incomplete fragment of colony from which to describe the new species.

1924. *Phylactella lyrulata.* Thornely, pp. 15, 16. Found ovicells but did not picture them nor materially add to the description.

1928. *Phylactella lyrulata.* Livingstone, pp. 73–75; photographs of colonies on Pl. VI, Figs. 1, 2, 6; and Pl. VII, Fig. 1. His text figures 16 and 17 show the inner frontal wall surface, lyrula, compensatrix muscles, occlusor muscles and very dried up polypide. He mentions operculum but does not figure it.

1952. *Phylactella lyrulata.* Vigeland, p. 10. Distribution only.

1956. *Phylactella lyrulata.* Rogick, pp. 226, 267, 300. Mentioned only in connection with other species.

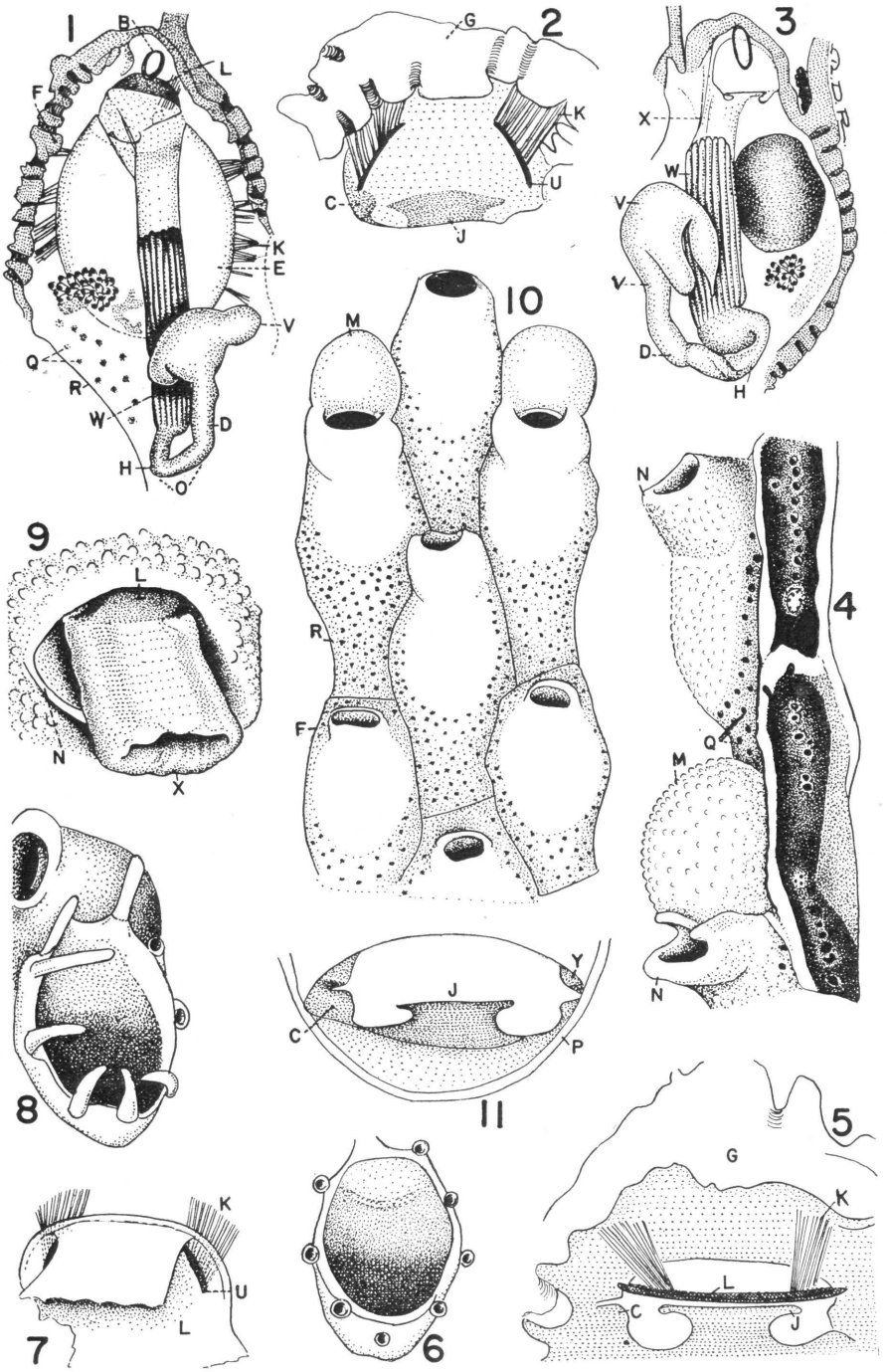
Key to abbreviations used on plates

A—Anus
B—Basal wall pore
C—Cardelle
D—Cardia
E—Compensatrix
F—Distal-lateral wall
G—End wall
H—Esophagus
J—Lyrula
K—Muscles
L—Operculum
M—Ovicell
N—Peristome
O—Polypide
P—Pore chamber in lateral wall
Q—Stellate frontal pore
R—Proximal-lateral wall
S—Pylorus
T—Rectum
U—Sclerite
V—Stomach
W—Tentacles
X—Tentacle sheath
Y—Ledge above cardelles

EXPLANATION OF FIGURES IN PLATE I

All figures on this plate are of *Phylactellipora lyrulata*, drawn with the aid of a camera lucida.

1. One zoid, seen from the basal surface, with nearly all the basal wall removed, except in the immediate vicinity of the basal pore (B). Polypide (W,H,O,D,V) withdrawn. Compensatrix (E) attached to the zooecial wall by several groups of parietal muscle fibers (K) around its periphery. The operculum (L) is in characteristic location, very close to the pore. Testicular mass shown to left of tentacles.
2. Operculum from the inner, basal aspect. Occlusor muscles (K) attach to sclerites (U) at one end and to zooecial wall at other end. The lyrula (J) is in front of (outside) the operculum.
3. Basal aspect of zoid whose body cavity contains an embryo, the large dark ball at right of the tentacles.
4. Side view of two zoids, the upper non-ovicelled, the lower with an ovicell. Lateral walls with their communication pores are darkened for contrast. The narrow front rim of the ovicell shows well as does the interruption of the peristome by ovicell.
5. Orifice from inner, basal aspect, with the operculum (L) open, at right angles, to the lyrula (J). Orifice appears shorter proportionately than it really is, due to the angle at which it is tipped.
6. Ancestrula. Eight spines broken off; ninth not yet developed.
7. Operculum. Its lower limit is indefinite. A strip of body wall was torn off with it.
8. A 9-spined ancestrula with its budded-off normal-looking zooecium. Two spines broken off.
9. Partly extruded tentacular sheath (X) with operculum (L) above it, a location characteristic of this species. Looking down on the peristome.
10. Seven calcined zooecia, two ovicelled, the rest not. The non-perforate front below orifice represents the compensation sac area. Pores on lower front stellate.
11. Orifice of ovicelled zoid seen from the outside. The cardelles (C), the grooves above them and the ledges (Y) above the grooves are typical but sometimes hard to see. Upper border of inner, primary orifice hidden by ovicell rim.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Diagnosis:—Zoarium partly encrusting. Zooecia large. Frontal a pleurocyst, with varying numbers of rows of stellate peripheral pores arranged in a crescent proximally. Basal wall with large oval distal pore. Lateral walls have 5 to 12 rosette plates or corresponding openings. Compensatrix occupies about half the frontal inner surface. Tubulous flattened peristome longer below than above orifice. Peristome entire except when globose imperforate ovicell is present to interrupt it. Lyrula low, broad, with corners sharply prolonged laterally. Cardelles with groove and ledge directly above them. Delicate, simple, incomplete operculum. Ancestrula 9-spined.

MORPHOLOGY

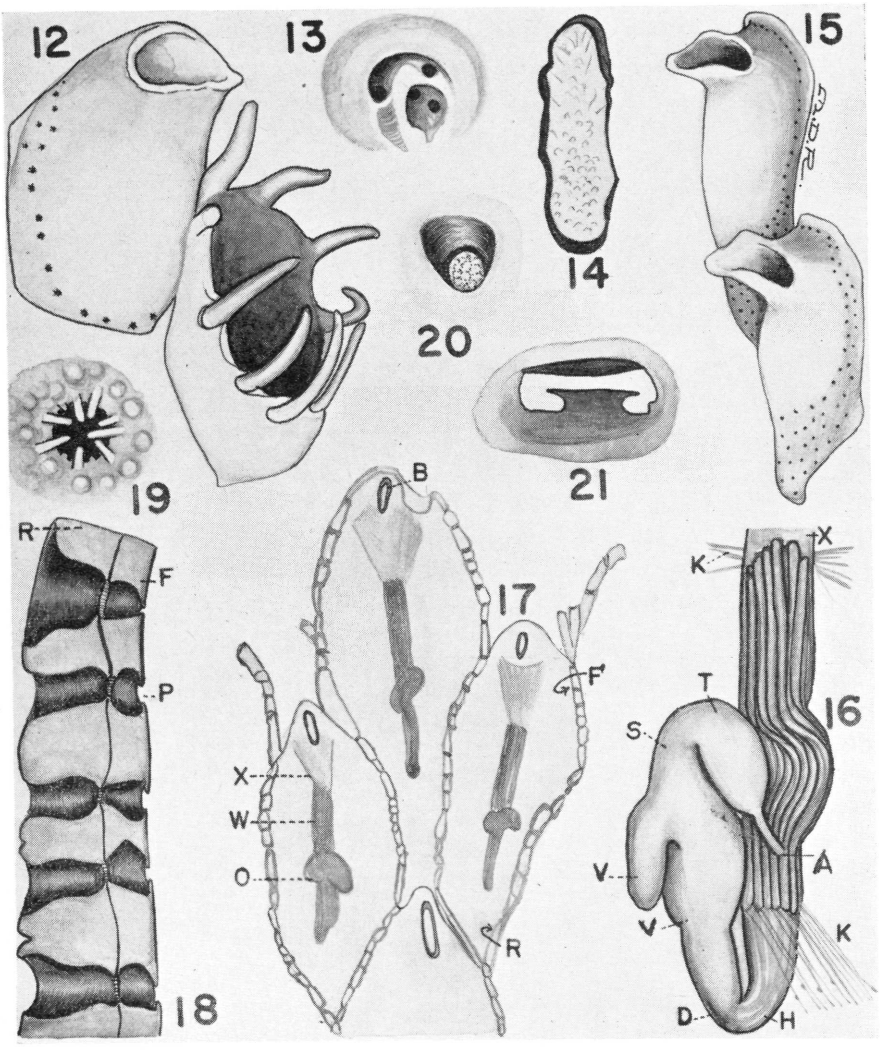
In calcareous bryozoa the external skeleton (zooecium) is sometimes the only part described and even that, most likely, very inadequately. Some of the taxa are founded exclusively on the exoskeleton. Soft internal parts as tentacles, gut, musculature, other organs and sometimes even opercula or other chitinous structures are often completely ignored even if there appears to be sufficient material. In some species the calcareous exoskeleton may be sufficiently transparent in places for the soft parts to show through it, as is the case in *P. lyrulata*, through whose back wall the soft parts can be studied to some extent. In many species, however, one must resort to decalcification or careful dissection and removal of exoskeleton before soft parts can be studied, procedures both time-consuming and resulting in the partial destruction of the specimen. Consequently , the internal anatomy of many recent calcareous bryozoa has never been fully investigated by taxonomists, so there remain many gaps in our knowledge. It is the purpose of the present series of papers to fill in as many gaps as possible for Antarctic species and to show the range of variation of which a species is capable, in so far as material permits.

Variations in size of individuals and structures are the easiest to study and are in some instances significant in differentiation between otherwise similar species. The measurements below give the range of variation for *P. lyrulata*, based on the USNM specimens. Previous authors have given no measurements whatever for this species.

EXPLANATION OF FIGURES IN PLATE II

All figures on this plate are of *Phylactellipora lyrulata*, drawn with the aid of a camera lucida.

12. Nine-spined ancestrula and typical second zooecium of the new colony.
13. Rosette plate with four pores from distal-lateral wall of zoid.
14. Chitinous membrane that plugs up the basal wall pore.
15. Two zooecia with unusually long urceolate peristomes.
16. Withdrawn polypide, tentacles slightly twisted in tentacle sheath. The short muscles (K) at top are the parieto-vaginals, while the lower, longer muscle fibers (K) attached to the lophophore or base of the tentacles are the retractors.
17. The basal surface of four zooecia. The basal wall pore (B) is next to the end wall in all cases. End walls are single, side walls are double partitions between zoids.
18. Detail of a double lateral wall as seen from the basal aspect. The thicker left wall (R), with its deeper channels or openings is the proximal-lateral wall of a left zoid. The thinner right wall, with its shorter, bulb-shaped rosette plates or chambers is the distal-lateral wall of a right zoid. The channels or pores are usually filled with soft parenchymous tissue strands.
19. Detail of a stellate frontal pore, which is generally round internally and partly bridged over externally.
20. Looking down into a communication canal and pore from the proximal-lateral wall. Compare with the side view of similar channels in left wall of figure 18.
21. Peristomie (channel), lyrula, cardelle and the darkened operculum above and parallel with the lyrula. This was the position of the operculum frequently found in zooecia which were empty of polypides, or where degeneration had set in.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Measurements:—The first figures are the minimum, the next the maximum readings; the last, in parentheses, are the average of all readings, 10 for each structure, unless otherwise specified. Length, width and height are abbreviated to L, W and H. All measurements are in millimeters.

1.517–1.924 (1.728)	L Zooecia, frontal view
0.851–1.036 (0.925)	W Zooecia, frontal view
0.144–0.202 (0.169)	L Peristomice (secondary orifice), inside measurement, somewhat foreshortened, as seen from front.
0.259–0.360 (0.296)	W Peristomice, inside
0.144–0.187 (0.167)	L Primary orifice, 3 measurements
0.288–0.360 (0.317)	W Primary orifice, 3 measurements
0.050–0.072 (0.065)	L Lyrula
0.086–0.173 (0.126)	W Lyrula at narrowest point
0.144–0.230 (0.175)	W Lyrula at widest point, tip
0.504–0.634 (0.583)	L Ovicell
0.562–0.590 (0.575)	W Ovicell
0.101–0.259 (0.170)	L Basal wall pore
0.072–0.158 (0.107)	W Basal wall pore
0.147–0.169 (0.159)	L Operculum, 4 readings
0.250–0.279 (0.264)	W Operculum, 4 readings
0.264–0.338 (0.298)	Embryo diameter

Zoarium:—The colony or zoarium may form extensive, brittle, calcareous chips. It may be unilaminate, bilaminate or even trilaminate. It is encrusting to foliaceous, its free edges crinkly. It may grow out in sheets or fronds. Its coarsely patterned surface is rough, like a file, because of the projecting peristomes of the large zooecia. Polypides and embryos are present.

Ancestrula:—The ancestrula looks quite different from the other zoids of the colony, resembling a Membraniporan zoid. It is 9-spined, has a large membranous frontal area and an imperforate gymnocyst surrounding the membranous frontal area. A larva can settle and produce an ancestrula on the frontal face of a living colony of its own species and thus in time give rise to an overgrowing layer of zoids. One zoarium, from Sta. 190, had a young colony of 6 zoids and ancestrula growing on it.

Avicularia:—Absent.

Zooecia:—The pentagonal to heptagonal zooecia (fig. 10) are thin-walled and large enough to see with the unaided eye. Their beaded frontal surface is convex, rising gradually to the urceolate peristome. The central, more elevated part of the front is imperforate. The peripheral part has numerous stellate pores arranged in a crescent proximally, in several rows (4 to 8). Their number diminishes laterally and distally to one or two rows (fig. 15). The pores are round on the inside wall surface but stellate on the outside (fig. 19) because of the delicate spicules jutting out over them.

Inconspicuous, faintly salient mural rims outline some of the zooecia.

The compensation sac (compensatrix) area occupies the inner surface of the non-perforate part of the frontal wall or about one half of the entire frontal (fig. 1). Livingstone described it but apparently did not grasp its significance. Numerous short unilaminate bundles of muscle fibers attach to the compensatrix at the boundary or periphery of the compensation sac area.

The basal wall of the zooecium is smooth, translucent, slightly convex. Near its distal end is a large, oval, membrane-covered hole, which is present in all zooecia (fig. 1, 3, 14, 17). Its chitinized border ranges from colorless to a deep brown. It is strange that a pore so large, constant in position and peculiarly located should have escaped the notice or comments of other workers. Its function is unknown but its location just opposite (directly behind) the orifice suggests that this membrane-covered uncalcified part of the basal wall may be of use in equalizing internal pressures when the tentacles and tentacular sheath are extruded or when being withdrawn into the zooecium.

The end walls are single and sinuous to acutely peaked.

The gently curved lateral walls have 5 to 12 rosette plates or corresponding openings per wall. No attempt is made to distinguish here between rosette plates and openings as defined by Levinsen (1909, pp. 27–28), although figure 18 does show the difference between them. The

rosette plates may be multiporous (fig. 13) or uniporous. They are arranged sometimes in a single row (fig. 4), sometimes in zigzag fashion.

Orifice:—In non-ovicelled zoids the secondary orifice (peristomice) is dorso-distal (fig. 4), ellipsoidal, wider than long and completely surrounded by an elevated, beaded peristome which is formed entirely by its own zooecium, *i.e.*, the next distal zooecium does not take part in its formation as is the case in some other species. The peristome is much longer proximally than distally, its lower lip urceolate, sometimes like a pitcher spout (fig. 15). In ovicelled zoids (fig. 4, 10) the peristome is interrupted distally by the ovicell, hence is incomplete. No oral spines present. The ancestrulae (fig. 6, 8, 12) are the only individuals with spines.

The primary orifice is somewhat reniform, deep within the peristome (fig. 2, 3, 5, 11, 21). A sinus separates the broad low lyrula on each side from the ledge-like cardelles. The cardelles were not mentioned by previous workers. Above the cardelles may sometimes be seen a groove and an obliquely slanting ridge. These may escape notice because of their slanting downward and back of the cardelles. The sharp thin corners of the lyrula are sometimes greatly extended laterally over the sinuses, even more so than shown in figure 5. Livingstone pictured the lyrula faithfully but missed seeing the cardelles, groove or overhanging ledge. It is very easy to overlook them.

Operculum:—The delicate, faintly chitin-edged (fig. 7), peculiarly located (fig. 9) operculum is difficult to see. In zooecia empty of polypides the operculum and its part of the body wall may remain attached inside the distal wall of the peristome (fig. 21). In zooecia with partly extruded tentacle sheaths (fig. 9), the operculum is above the tentacle sheath—a position less common than that in other operculate bryozoa where the usual position for the operculum is below or in front of the tentacle sheath.

The operculum is somewhat hemispherical. Its outer curvature is slightly chitinized (fig. 7) but its inner, proximal border is essentially non-delimited. A slender chitinized sclerite is obliquely set some distance in from each lateral border. To it attaches a row of sturdy thickly set opercular (occlusor) muscles (fig. 2, 5, 7). So far as can be determined, the opposite ends of these muscles seem to attach near the junction of the lateral, basal and distal walls, but the exact location requires further study. Examination of the fibers with phase contrast did not reveal any striations in the muscle fibers.

Ovicells:—The ovicells are globose, salient, finely beaded, imperforate (fig. 4, 10). The neighboring zooecial fronts do not encroach upon the ovicell, nor do the peristome walls. The latter only meet the ovicell, which interrupts the peristome. Not all zoids had ovicells but ovicells were present in material from most stations. Practically all but a very few were empty of any embryo. More zoid body cavities than ovicells had an early embryo at the time of collection (fig. 3).

Polypide:—The polypide (fig. 16) consists of the tentacles, tentacle sheath, digestive tract and associated musculature. The digestive tract folds up along side the tentacles when the latter are retracted. The tentacle sheath is long, and the anus opens into it. The digestive tract consists of mouth, pharynx-esophagus, cardia, pyloric zone of stomach, coecum (caecum or cul-de-sac) part of stomach, rectum and anus. The pharynx-esophagus is about as long as the cardia but thicker-walled than the rest of the tract. The esophagus, cardia, stomach and rectum are yellow. The tentacular sheath, tentacles, oropharyngeal zone are darker. Retractor muscles attach to the lophophore region at the base of the tentacles. As in the occlusors, no striations could be seen in the fibers under phase contrast but the material was not fixed or specially stained to make sure.

No oral glands are present in the opercular region.

Since nearly all zoids were retracted the tentacle number could not be accurately ascertained, but it did appear to be greater than 12 and less than 20.

Livingstone (1928, p. 73, fig. 16) pictured a polypide but it must have been a dried up specimen because it is rather misleading. However, he is the only predecessor who made an earnest attempt to study the soft parts in this species.

A spermary occurred in both ovicelligerous and non-ovicelled zoids but did not seem to be present in all zoids examined. Whether this is because some zoids may be asexual or whether gonads are only temporary structures could not be determined at this time. Spermaries were

seen in some zoids which seemed in their prime and in other zooecia whose polypides had largely degenerated. A small, lumpy, band-like ovary is present in a few ovicelligerous zoids near the spermary. The spermary is larger, more definite and shaped like a raspberry (fig. 1, 3). It is at the side of the body cavity, near the side wall, some distance away from the digestive tract.

Some ovicelled zoids had a single large developing embryo in the body cavity, in addition to the spermary, so must have been hermaphroditic. As the embryo increased in size the polypide degenerated. No fertile zoid had more than one sizeable developing embryo in it at the same time.

DISTRIBUTION AND ECOLOGY

To date, *Phylactellipora lyrulata* has been collected only from Antarctic localities and from depths ranging between 25 to 354 fathoms (Livingstone, 1928, p. 75). The USNM specimens came from depths of 35 to 58 fathoms, from Antarctic stations Nos. 101, 104, 190, 225, 226, 230, 234, 236 and 243, between Jan. 29 and Feb. 22, 1948. Stations 101 and 104 are off Cape Royds, Ross Island; Stations 190 thru 243 are from Marguerite Bay, Antarctica. For full station data see Rogick (1956, pp. 222–223).

Phylactellipora lyrulata seems to be a species very adaptable to life on or with other organisms, because it is frequently found either growing on some other form or vice versa. Other species grow sometimes on its face, sometimes on its back, on either living or on dead colonies. Some of the bryozoan species which grow on *P. lyrulata* are *Barentsia discreta* (Busk) 1886, from Sta. 190, (Rogick 1956, p. 227); *Beania*, Sta. 234; *Cellepora milleporoides* Calvet 1909, Sta. 234; *Cribrilina spatulata* Calvet 1909, Sta. 236; cyclostomatous bryozoa, Sta. 226, 234, 236; *Lepralia marginata* Calvet 1909, Sta. 225; *Microporella parvipora* Waters 1904, Sta. 226; *Ramphonotus inermis* (Kluge) 1914, Sta. 226, 234; *Smittina ordinata* (MacGillivray) 1895, Sta. 226 (Rogick 1956, p. 300). Other forms which grow on *P. lyrulata* are both calcareous and mud worm tubes, sponges and hydroids. In turn, *P. lyrulata* was found growing over a calcareous worm tube from Sta. 190, entangled on a starfish from Sta. 243 and on the bryozoans *Cellarinella roydsi* of Sta. 234 (Rogick 1956, p. 267), *Schizoporella tumida* var. *tricuspis* Calvet 1909, Sta. 226 and on other species yet to be identified.

Specimens of *P. lyrulata* are on deposit with the Smithsonian Institution, USNM Cat. Nos. 11347 thru 11350 and 11352.

SUMMARY

1. *Phylactellipora lyrulata* is reported from additional Antarctic localities.
2. Measurements of many structures are given for this species, none having been available heretofore, to show the range of size variation.
3. The peculiarly located operculum is figured fully.
4. Livingstone's description and sketches of the polypide (gut) are modified and augmented.
5. Other species in the present collection incidentally reported from additional Antarctic localities are: *Cellepora milleporoides*, *Lepralia marginata* and *Microporella parvipora*.

ACKNOWLEDGMENTS

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Remaining incidental citations are fully listed in Rogick 1956 "Literature Cited" section, and are not here repeated.